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ELIZABETH BANGS BRYANT

April 7, 1875 — January 6, 1953

PSYCHE

Vol. 65 March, 1958 No. 1

ELIZABETH BANGS BRYANT

By Elisabeth Deichmann

Museum of Comparative Zoology

It was some years after I had come to Cambridge that I first met Miss Bryant. At that time (1926) the entomologists had their own entrance, and simply going around and making calls was not encouraged. But after Thomas Barbour became director (1928) and after the Biology Department had moved across the street, she and I became neighbors on the fourth floor. She discovered that I made tea for my lunch and suggested that I come in and drink tea with her, and for more than 15 years I usually had lunch with her about three times a week. She must have been about sixty when we first met and she seemed to change very little with the years. She was of medium height, fairly stout, with regal carriage. She had unwrinkled skin, clear blue eyes and white hair. In some quarters of the museum she was referred to, not unkindly, as "Queen Victoria" and although much taller and with a decidedly retroussé nose, her black dress, snow-white hair and somewhat pendulous cheeks gave her a certain resemblance to that lady. She is the only person I have known who used the word "twaddle", and that with as much emphasis as I imagine Queen Victoria did. Behind her sedate exterior she kept a rather youthful spirit. She was extremely well read with a rich vocabulary of old Yankee expressions and after she had used one of these she would suddenly pretend that she was embarassed: "Oh, Miss Deichmann, I really should not teach you such language!"

It is perhaps quite characteristic that I never had the slightest idea of what her father had been, while I was

extremely well acquainted with the famous cat of her childhood, so dignified that she and her brother always referred to it as *Mister* Verdant Green. She belonged to a good substantial Boston family and seemed to be related to a large number of prominent persons, which did not prevent her from expressing her, not always high, opinion of these relatives. She had evidently had an extremely happy childhood and a youth filled with trips to Europe and the typical Bostonian's cultural interests. The family had even been so progressive that they had allowed her to go to Radcliffe, which definitely was the great adventure of her life, as for all women of her generation who suddenly were allowed to get the same education as their brothers. She belonged to the class of 1897 but she did not graduate. There may have been illness in her family, or it may have been just at that time that her family, as well as many other substantial Bostonians, were rather hard hit financially. Her interests were with natural history and she became early acquainted with the men in the Boston Natural History Museum and those connected with the Agassiz Museum, and in the latter institute she was soon given the little division of spiders to take care of. In her younger days she was an eager field worker: there was a widespread interest in nature study in Boston and she took part in many botanical and zoological excursions and built up quite a collection of New England spiders. Her father died rather early and after that time she took care of her mother for many years, while she regularly appeared in the Agassiz Museum three times a week, but her outdoor activities became quite naturally restricted and her circle of acquaintances limited to men much older than herself, Mr. Samuel Henshaw, Mr. Faxon and especially Mr. J. H. Emerton, who was delighted to see a younger person take over in the spider field.

In the museum she had been fortunate to be allotted a small division. With the myriapods and mites in two neighboring rooms, she was able to have all the spiders around her. She learned to type and besides she wrote hundreds of cards and labels in her precise, clear hand. Her reprint collection was well cared for, with binders which

she bought herself. Her first paper came in 1908; it was merely a list of local species, but it had probably taken some persuasion from her good friend, Mr. Emerton, to let her to allow her name to appear in print. It was 15 years later that her Barbados-Antigua report was published, and then, around 1930, she really began to be a regular contributor. Very likely it was the stimulus she received when Dr. Barbour saw to it that this volunteer worker of almost 30 years standing at last received a small salary. She steadfastly refused to be listed in American Men of Science, feeling that that was to intrude into the ranks of professionally trained, and no argument could change her position on that point. It was a great joy to her when other arachnologists visited her and she was always helpful to beginners who came to seek her advice. When somebody brought in a spider she would tell all about its habits and occurrence, and she never crushed the collector with a remark that it was one of the most common forms. "It is such a long time since I have had occasion to see a live specimen of this spider," — so the person went off feeling that his efforts had been fully appreciated.

Her main scientific work was not started until she was 55 years old, and continued to her death. Several large papers on West Indian spiders were illustrated by her clean pen drawings. She was handicapped in her work by an inadequate microscope and light (a modified automobile spotlight). She worked independently of all but a few colleagues in arachnology.

For several years her mother's health was failing and she looked after her with unswerving fidelity. After her mother's death she moved from the house in Allston to a pleasant top floor apartment in Brookline. It looked as if she was going to have more freedom and our long planned trip to St. Lucia in the West Indies, the type locality for so many of the West Indian spiders, seemed near to becoming reality, when the old housekeeper's health gave out and Miss Bryant undertook to care for her, most scornful of the idea that the housekeeper should be put in a Nursing Home.

There was one unusual activity in which Miss Bryant

indulged, and that was taking care of her investments. After her father's death, her mother, mindful of the debacle of some years before, made arrangements, so that she got a fixed income and divided the family fortune between the two children. That was in the happy days before the income tax had been invented. The usual course would have been that Miss Bryant's share be put in a trust fund, but here her old friend, Mr. Henshaw, intervened. She took, as always, his advice and developed into an extremely shrewd and careful investor. Through her interest in her investments, by reading newspapers and magazines, she acquired an unusual understanding of what was going on in the United States and in the world as a whole, and her down to earth realism and a total lack of sentimentality made conversations with her extremely interesting.

In addition to her indisputable business ability, which would have made her a gift to a brokerage firm, she possessed also the virtue, thrift. She saw to it that nothing was wasted in her house, got the utmost wear out of her few garments and she kept all unnecessary expenditures down to zero. She subscribed to a few magazines which she knew she could manage to read, and the back numbers were quickly passed on to some other person for whom she was happy to save the cost of a subscription. While despising people who made themselves miserable by being "penurious" she enjoyed her own little pet economies. For years she would happily trot down a few blocks so that she could get home on the 5 cent fare, and until her last illness it was our monthly joke when she handed me her check for the Faculty Club and asked me to take it over to Harvard Square when I was paying my own bill, adding with mock seriousness: "I just can't *bear* spending 3 cents on such a short distance, and the bus no longer sets me off in Harvard Square."

She felt her responsibility toward the needy, particularly children and old people, and she insisted on knowing where the money went. She saw to it that nothing was lost between her hand and that of the recipient. She lived for years in a rather poor district where as she once expressed it: "They are counting on my contribution" — and they got it. At

one time an over eager Community Chest agent tried to persuade her to give her large contribution through the Museum instead of just the token which she usually gave. But she was adamant, her contribution was going to where it had been going for years, long before the Community Chest had been established. The argument became rather heated: "It was her duty toward the Museum." Then Miss Bryant got up: "My resignation shall be on the Director's desk this afternoon!" The subject was quickly dropped.

When she had been fifty years out of college she received an honorary Phi Beta Kappa membership from Radcliffe as the one of her class who had made the most out of her education, and this was a great pleasure to her. But she appreciated it even more when, at about the same time, she was taken into the Radcliffe Sigma Xi, for this enabled her to get into contact with young people, a pleasure which her duties toward her mother had prevented for years. Contrary to her custom of never going out in the evening, she would attend all their evening meetings.

She continued working after her retirement in 1950, it seemed almost with even greater vigor than before. Several years before that time the difficulties the museum had, and still would have for years, regarding decent pay to the curators were clearly seen by us all; she had also seen how the Boston Natural History Museum had packed several collections aside and had given others away to where they could be used, and she realized that a similar fate might well befall the collections which she was in charge of. Suddenly she realized that she was able to act so that this should not happen. It was with deep emotion that she one day came to me and told me that she had radically altered her will so that the work could go on after her death and she was a changed person from that moment. Her plans for her work became bolder and she decided to get a new and better microscope even at this late time of her life.

It was when I came home from a trip in the fall of 1952 that she informed me that she was not feeling well and that an operation was necessary because of stomach cancer. After the operation I saw her two or three times a week at her home and our conversations went on almost as if she

were still in her office in the Museum. She admitted she was feeling oddly "lighthearted" and there were a few moments when she almost believed that she might get well enough to come back for a short time and do a little work. But when her new microscope at last arrived she sent it straight back to the Museum. At first she was well enough to get up and come out and wave goodby to me on the stair case, later she asked to be excused. The end came on January 6, 1953.

Her will was a model of careful consideration of the needy in the community and her family. Two of the larger bequests, of equal amounts, went to Radcliffe College, which had given her her education, and to the Museum, where she had been able to make use of it. With her usual reticence she had in the latter case succeeded in keeping her name hidden. The bequest was simply named the "Emerton Fund" in honor of the old arachnologist who had taught her to draw and encouraged her in her work.

There were also two small bequests each of 500 dollars to the two Radcliffe Honor societies. In the case of Phi Beta Kappa the money helped to hasten the completion of the $10,000 Scholarship Fund which this old and fairly wealthy chapter had been working on, and her name was duly added to the Memorial Roll. In the case of the much younger, smaller, and anything but wealthy Chapter of Sigma Xi, the sum, with interest and smaller gifts added, was some years later voted to be used as the nucleus of a much needed loan for Radcliffe science students, and was named the "Elizabeth Bangs Bryant Loan Fund of Sigma Xi."

The following is the known list of her publications:

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OOGENESIS AND FERTILIZATION IN *THERMOBIA DOMESTICA* (PACKARD)[1]

By John T. Woodland

State Teachers College, Salem, Massachusetts

The materials and methods used in this study were the same as those described in an earlier paper (Woodland, 1957).

Oogenesis

The primary oocytes in the vitellarium reach a length of about 420 microns just before yolk accumulation begins. They measure only about 45 microns wide. Each has a large central nucleus about 40 microns in diameter. It is a typical vesicular oocyte nucleus and usually has a visible nuclear membrane. A fine network is visible throughout the nucleus and there is a large, eccentric, irregular, granular nucleolus which may be as long as 20 microns. Neither network nor nucleolus is Feulgen-positive. The finely-divided chromatin is so scattered throughout the large nucleus that it is barely visible. The cytoplasm appears very finely granular and contains a few inclusions. These are 10 to 15 microns in diameter and consist of a dozen or less clumped globules.

When each of the vitellaria contains four or five of these oocytes, yolk accumulation begins. It starts peripherally in all of the oocytes simultaneously and gradually proceeds toward the center. There appear scattered through the peripheral cytoplasm tiny globules which stain bright orange-red with Mallory's triple stain. They greatly resemble the globules of protein reserves scattered through the fat body surrounding the ovarioles, but are usually a little smaller. The negative images of small fat droplets also occur in the peripheral cytoplasm. The fat droplets and proteinaceous globules increase in size, forcing the diminishing cytoplasm into a network around them. By

[1]The research was carried out at the Harvard Biological Laboratories, Cambridge, Massachusetts, in partial fulfillment of the degree of Doctor of Philosophy.

the time that small fat droplets begin to appear in the center of the oocyte, the peripheral droplets and proteinaceous globules have greatly enlarged (3 to 7 microns in diameter) and are present in about equal numbers. The diminishing central layer of cytoplasm around the nucleus is connected by the fine network between the yolk globules to a thin peripheral cytoplasmic layer, the periplasm. By the time the perinuclear cytoplasm has become very thin, the fat droplets appear to have coalesced, for the visible proteinaceous yolk globules, some of which are now as large as 11 microns in diameter, stand out in fixed preparations against a clear background.

The oocyte has been growing only slightly meanwhile, and is still very narrow in proportion to its length. Before oviposition the maximum length of the egg increases by about two and one-half times, and its maximum width increases about eighteen times. Growth is accomplished chiefly by an increase in the proteinaceous yolk. Just before oviposition the egg contains relatively little fatty yolk.

At the start of the growth period the nucleus moves to the periphery. The nuclear network condenses at the periphery of the nucleus and the chromatin becomes distinctly visible with the Feulgen technique. Evidence of tetrads is seen. The interior of the large nucleus now appears homogeneous and has little affinity for the stains used. Before oviposition there occur both a marked decrease in nuclear volume and further condensation of the chromatin into small compact chromosomes.

The follicle cells start to secrete the endochorion at the time when yolk accumulation first begins. The process is best studied in preparations stained with phosphotungstic hematoxylin. Just before secretion of the endochorion starts, the brown-staining connective tissue sheath surrounding the ovariole becomes greatly thickened. It appears that the follicle cells withdraw material from the sheath and secrete it to form the endochorion. Comparison with the accompanying process of yolk accumulation indicates that the sheath is reduced to its former size within a relatively short time. The secretion of the exochorion, which occurs much later, is mentioned below.

The external appearance of the newly laid egg of the firebrat has been described by Adams (1933), Sweetman (1938), and Remington (1948). The present study reveals that the endochorion (Fig. 5, EN) is about 2 microns thick. Its thickness does not vary appreciably over the whole egg. There adheres to its outer surface a single layer of spherical droplets, each about 11 microns in diameter immediately after oviposition. The droplets are rather irregularly placed, but tend to be in groups with large intervening spaces. In the spaces are droplets many times smaller than the large ones. Within a few hours a change occurs. The large droplets break up into rather evenly spaced ones about 3 microns in diameter (Fig. 5, CD). Usually a space of 2 microns now occurs between droplets, although pairs of contiguous droplets are sometimes seen. The very minute droplets are still scattered among the larger ones. The appearance of the droplets is essentially the same on shed chorions long after the nymphs have left them. Possibly the droplets are present as a thin continuous film before oviposition.

The droplets adhere firmly to the exochorion. A few individual droplets are separated from it by sectioning, but the other procedures to which the eggs have been subjected practically never dislodge them. In contrast, the exochorion is loosened from the endochorion when the egg contents shrink during fixation, owing to dissolution of the fatty elements. Moreover, the exochorion is normally loosened from the endochorion during development, as the volume of the egg contents is diminished slightly. The surface of the endochorion is then seen to be reticulated into hundreds of small polygonal areas. Most of these polygons are fairly regular hexagons with diagonals usually between 55 and 85 microns long. The wall separating adjacent areas is 5 microns thick.

Sweetman (1938) supposed this hexagonal reticulation to be produced by the cells of the embryonic tissues, but the present study showed it to be produced by the follicular cells that secreted the endochorion. The large size of the hexagons emphasizes the amount the egg has grown since the endochorion was secreted.

The endochorion is hardly ever loosened at all from the yolk and no vitelline membrane has been found between them. Heymons (1897) reported a vitelline membrane in *Lepisma saccharina,* but Uzel (1898), who studied the eggs of the same lepismatid, did not mention it.

Between the exochorion and the endochorion at the anterior end of the egg is the micropylar area, a circular thickening about 280 microns in diameter (Fig. 5). The thickening consists of as many as twenty or more concentric lamellae, each about as thick as the exochorion, with which the thickening is identical in staining reactions and to which it adheres if the latter becomes loosened from the endochorion. The thickening is thinner peripherally than centrally, since not all of the lamellae extend to the margin of the area.

In the micropylar area are found three small infundibular depressions which, if connected, would form the corners of an equilateral triangle. Two of the depressions are shown in figure 5 (DP). The depressions, which can rarely be demonstrated to penetrate the micropylar thickening completely, are filled with folds of the exochorion and with the chorionic droplets described above. There sometimes ap-

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Explanation of Plate 2

All figures represent portions of sections. Fixative: Maximow's. Stain: Feulgen's all figs. except 2 and 5; Mallory's triple, figs. 2 and 5. Magnifications approximate. Fig. 1. 20 minute old egg, showing sperm head accumulating cytoplasm, 400 x. Fig. 2. 30 minute old egg, showing egg nucleus in anaphase of first maturation division, 500 x. Fig. 3. 2½ hour old egg, showing egg nucleus in anaphase of second maturation division, 500 x. Fig. 4. 75 minute old egg, showing late telophase of first maturation division; secondary oocyte nucleus forming in upper left, first polar body in lower right; 500 x. Fig. 5. Longitudinal section through micropylar (anterior) end of 2 hour old egg, 160 x; CD, chorionic droplet; DP, depression; EN, endochorion; EX, exochorion; EXT, exochorionic thickening. Fig. 6. 90 minute old egg, showing late stage in the contraction of the sperm head, 1250 x. Fig. 7. Egg about 2 hours old, showing male pronucleus during its growth period; 1875 x. Figs. 8-11. 3 to 4 hour old eggs, 1250 x. Fig. 8. Early stage of union of male and female pronuclei. Fig. 9. Female pronucleus shown near top just enteriing the sperm plasm; male pronucleus (below). Fig. 10. Female pronucleus (below) and male pronucleus (above) about to unite. Fig. 11. Late stage of union of male and female pronuclei.

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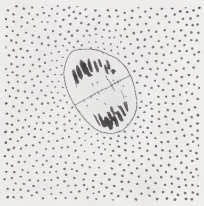

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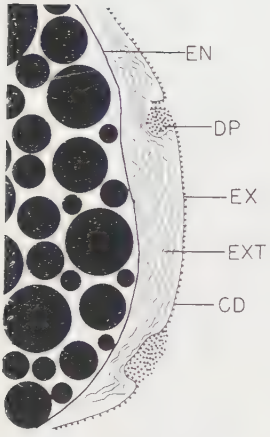

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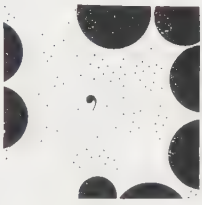

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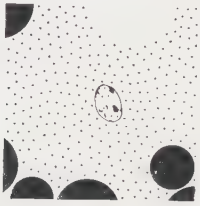

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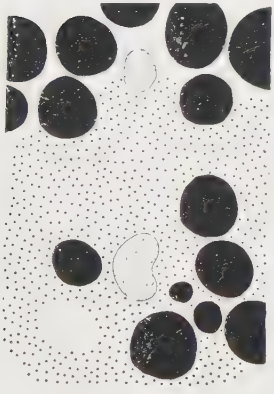

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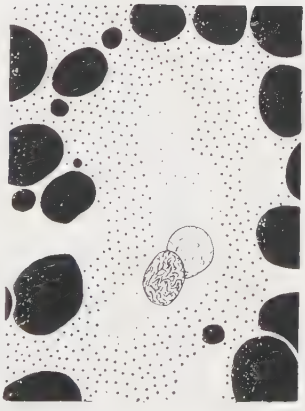

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WOODLAND — THERMOBIA DOMESTICA

pears to be an opening through the exochorion where it dips into a depression (Fig. 5), but no opening through the endochorion was found. Other evidence suggests that there is none. Eggs completely immersed in tap water at 37.5° C. for a period of 3 or 4 days during incubation hatch into healthy nymphs in about the normal time. (Hatching itself occurs under water, but the nymphs cannot get their abdomens out of the shell. This is because they cannot get traction and also occurs in a small percentage of eggs hatching in an empty glass container.) If openings completely penetrated the chorion, then water should be expected to enter the egg by osmotic pressure and cause it to burst. If eggs are kept in tap water for as long as seven days, the incubation period is prolonged by several days and only about half of the eggs hatch at all. Those not hatching do not burst nor are they turgid. Presumably they die from oxygen lack, as the water was not mechanically oxygenated.

The follicle cells appear to become a syncytium during the enlargement of the oocyte. This syncytium probably secretes the micropylar thickening and the thin structureless exochorion just before the oocyte leaves the ovariole. The chorionic droplets are believed to be added as the egg passes through the lateral oviduct, for droplets of similar appearance have been seen in the cells of the oviducal epithelium of females with large oocytes in the ovarioles.

Fertilization

After the oocyte leaves the gonopore but before it proceeds down the ovipositor, it is undoubtedly held at the base of the ovipositor for a few moments while sperms are discharged onto it by the spermatheca. The sperms presumably enter the probable openings in the exochorion over the depressions in the micropylar thickening. They can apparently penetrate the endochorion directly. They would not have to penetrate the endochorion directly under the micropylar thickening, but could pass between the lamellae of the thickening and enter nearer the equator of the egg. Whether the entire sperm penetrates the egg was not determined. Within the freshly laid egg, however, may usually be identified from one to six of the very long sperm heads,

each of which is bent and coiled upon itself many times.

The contents of the living, freshly laid egg appear to consist of colorless yolk spheres in a colorless liquid of low viscosity. The spheres are about 10 to 15 microns in diameter. In sections of eggs fixed with Maximow's fluid the negative images of the fat spheres measure 9 or 10 microns in diameter. Most of the more numerous, visible, proteinaceous yolk globules are 14 or 15 microns in diameter. Some of these globules appear structureless, while others appear finely granular. The globules appear only very slightly flattened at the poles with Maximow's fixative. The other fixatives used always badly distorted the yolk of young eggs. The yolk spheres and liquid fill the entire egg. Cytoplasm was not identified.

Perrot (1933) stated that the first maturation division occurs while the oocyte is still in the ovariole. He was not able to find any trace of the prophase of the division. He reported that the mitotic figure occupies a very small space at the periphery of the oocyte and figured the anaphase of the division. He stated further that after this first maturation division the nucleus enters a resting stage which he figured from a freshly laid egg. The present study did not confirm this part of Perrot's work. The only mitotic figures ever found in sections through the vitellarium were those of the follicle cells. The anaphase of such follicular mitoses often resembles that shown in the first of Perrot's figures just mentioned. Eggs fixed immediately after oviposition show the nucleus to be in the metaphase of the first maturation division. No nucleus resembling both in appearance and position that shown in the second of Perrot's figures was found until the beginning of the formation of the primary epithelium.

The anastral type of meiosis occurs. The mitotic figure is located more or less equidistant from the two poles of the egg, usually from 1 to 10 microns from the surface. The spindle axis is usually oblique to the egg surface, but is occasionally parallel to it. The distance between the two poles of the mitotic figure in metaphase and in anaphase (Fig. 2) is about 20 microns. The metaphase plate is about 8 microns in diameter. The chromosomes are very small

and close together. During telophase the mitotic figure is no longer fusiform, but is a spheroid with long axis about 14 microns long and short axis about 10 microns long. In presumably slightly older eggs a very distinct equatorial constriction is evident. The two groups of chromosomes separate to a distance of almost 30 microns. In favorably sectioned eggs most of the eighteen dyads in each group can be distinguished (Fig. 4). Many of the chromosomes are very short and V-shaped, so that the dyads look superficially like tetrads.

The first polar body is not extruded from the egg and does not divide. Its chromosomes never become surrounded by a nuclear membrane as do those of the secondary oocyte. The dyads gradually change into an irregular mass, which remains close to the surface of the egg and disappears relatively quickly. No certain trace of the first polar body was found later than the anaphase of the second maturation division.

The egg nucleus was never found in a resting stage between the maturation divisions. The spheroidal prophase nucleus, with its still distinguishable dyads, is believed to increase in size, since a series has been found with long axis varying from 8 to 15 microns in length. The second maturation division resembles the first in size and orientation, but its chromosomes are slightly more easily distinguishable (Fig. 3). The second polar body degenerates as does the first and has not been seen with certainty later than the four-celled cleavage stage. The chromosomes of the female pronucleus enter a resting stage with distinct nuclear membrane. The nucleus is a spheroid with long and short diameters of 9 microns and 5 microns respectively. It shows hardly any variation from egg to egg.

In the majority of freshly laid eggs, cytoplasm is seen starting to accumulate around one of the sperm heads (Fig. 1). This sperm and its sperm plasm are typically found on the longitudinal axis of the egg, about one-third of the way from the posterior pole to the anterior pole. The distance from the maturation spindle is roughly 400 microns. If several sperms are present in the egg, cytoplasm may or may not accumulate around more than one. In cases where

cytoplasm accumulates around from two to six sperms, their distribution is such that they are about equidistant from each other and from the surface of the egg. Just as much cytoplasm accumulates around a sperm whether it is the only one accumulating cytoplasm or whether five others are doing likewise. Accumulation of the sperm plasm ceases at about the time the oocyte nucleus has completed its first maturation division. By that time the sphere of sperm plasm is about 45 microns in diameter.

As cytoplasm accumulates around a sperm head, the latter undergoes a gradual decrease in length, with accompanying uncoiling and moderate increase in breadth. The Feulgen reaction indicates a simultaneous concentration of desoxyribonucleic acid toward the anterior end of the shortening sperm head (Fig. 6). Shortening continues until all that is visible within the sperm plasm is a minute nucleus about $1\frac{1}{2}$ microns long. This male pronucleus is formed at about the time that accumulation of sperm plasm ceases. While the egg nucleus is undergoing the second maturation division, the male pronucleus gradually enlarges (Fig. 7) until it is about 8 or 10 microns in diameter (Fig. 9).

The female pronucleus then migrates from its peripheral position to the sperm plasm (Fig. 9). When fixed before it reaches the sperm plasm, it is found to be rather irregularly elongated in the direction in which it was presumably travelling. Cytoplasm has never been identified around it. Both male and female pronuclei are approximately the same size and their finely divided chromatin appears very similar. Fortunately they can easily be distinguished when the Feulgen reaction is followed by light green counterstain. The nuclear sap of the male pronucleus shows great affinity for light green, while that of the female pronucleus shows practically none at all. It appears further that the movement of each nucleus within the sperm plasm just prior to fixation can be detected. For adjoining each nucleus fixed at this stage is a palely-staining streak which is interpreted to indicate the path over which the nucleus has just passed (Fig. 10).

As the female pronucleus enters the sperm plasm the sperm nucleus starts to move toward it. The two pronuclei

come together and their nuclear membranes break down where they are in contact with each other (Fig. 8). At the same time the chromatin of each condenses into a fine spireme. The nuclear sap of the female pronucleus simultaneously develops an affinity for light green, so that the two pronuclei can no longer be distinguished. The spiremes of the two nuclei become coarser and intermingle before any distinct chromosomes are visible (Fig. 11). The maturation divisions occupy about one and one-half hours each. Union of the pronuclei occurs during the fourth hour after oviposition.

Affinities of Lepismatids

The lepismatids for which both embryological and morphological data are available are *Lepisma saccharina* L. (Heymons, 1896, 1897; Uzel, 1897, 1898), *Thermobia domestica* (Packard) (Woodland, 1952, 1957; Sahrhage, 1953; Wellhouse, 1953), and *Ctenolepisma lineata* Fabricius (Woodland, 1957). All three belong to Subfamily Lepismatinae. The data indicate that *Thermobia domestica* and *Ctenolepisma lineata* are very closely related to each other and less closely related to *Lepisma saccharina,* which is more primitive than they.

Thermobia domestica and *Ctenolepisma lineata* differ embryologically from *Lepisma saccharina* in that in them the germ disk is formed at the extreme posterior end of the egg, radial symmetry is maintained until the germ disk starts to elongate, the embryo does not sink bodily into the yolk, the amniotic pore is not closed by a chitinous plug, and spiracle anlagen are not found on the ninth and tenth abdominal segments. Adults of *Thermobia domestica* and *Ctenolepisma lineata* differ from those of *Lepisma saccharina* by lacking parameres and by possessing ventricular caecae, an anterior projection of the vas deferens beyond where the most anterior pair of vasa efferentia empties into it, and often a third pair of styli. In the former two species the vasa efferentia of the members of a pair of sperm tubes do not unite before joining the vas deferens and the free end of one member of each pair of sperm tubes is directed mediad, while the free end of the other member is directed laterad. In addition, the lateral oviducts are relatively

shorter than in *Lepisma saccharina*. The author considers all of these characters to be secondary or specialized ones. Remington (personal communication, 1949) has noted several taxonomic characters as evidence for considering *Lepisma saccharina* more primitive than the other two species: the cephalic hairs of the former occur singly and do not bear secondary hairs, while those of the latter occur in groups and bear secondary hairs; also, the former has a less well developed ovipositor.

In spite of the close relationship between *Thermobia domestica* and *Ctenolepisma lineata*, each has a few specialized characters not shared by the other. In *Ctenolepisma lineata* a modified morula stage is absent, synchrony of cleavage is maintained longer, and intravitelline separation occurs late. In *Thermobia domestica* the amnio-serosal folds develop only weakly and there is a transverse division of the distal segment of the maxillary palpus.

Although the embryology of lepismatids and symphylans appears superficially very different, owing to the difference in relative amounts of yolk in the eggs of the two groups, actually a great deal of embryological affinity exists between them. Some of the characters shared by *Thermobia domestica* and the symphylan *Hanseniella agilis* (Tiegs, 1940) are of particular interest: (1) The polar bodies are not extruded from the egg and degenerate rapidly. (2) A vitelline membrane is not apparent. (3) Periplasm has not been identified in freshly laid eggs. (4) The inner layer is entirely mesodermal and is produced without the formation of a ventral groove. (5) The time and manner of segregation of the germ cells are similar. (6) The surface cells secrete a cuticle, in *Hanseniella* before germ band formation, in *Thermobia* after germ disk formation. (7) The midgut epithelium is derived from yolk cells. (8) The neuropile of the nerve cord is not covered dorsally by nerve cells. (9) Fourteen post-cephalic segments occur in the adult. Anamorphosis occurs in *Hanseniella* but not, of course, in *Thermobia*. It may be noted, however, that *Hanseniella* hatches with 8 post-cephalic segments followed by a pre-anal and an anal segment. During anamorphosis 4 more segments differentiate in front of the pre-anal seg-

ment. In *Thermobia* a distinct pause occurs after differentiation of the first 5 abdominal (first 8 post-cephalic) segments. The cercus-bearing (pre-anal) and anal segments are prominent during the interval before the remaining abdominal segments are differentiated in front of them.

The characters in which *Hanseniella* differs from *Thermobia* may be grouped into several categories. Examples of characters with homo'ogs in some primitive or generalized insects, but not in *Thermobia,* are: (1) Paired arteries arise from the aorta. (2) The presence of eversible sacs and coxal styli. Homologs of both of these structures are present in *Machilis.* In *Hanseniella* the two halves of the nerve cord arise laterally from the floor of the germ band rather than medially as in *Thermobia.* In *Hanseniella* the medial position is occupied by the "ventral organs" from which the eversible sacs arise. Examples of characters more primitive than those found in primitive insects are: (1) The adult has abdominal legs. (2) Only one pair of Malpighian tubules is present. (3) The labial segment is at first not part of the head. A few of the characters of *Hanseniella,* such as the secondarily acquired progoneate condition and the development of fat body from yolk cells, seem to express affinity with diplopods or as the incorporation of a pre-antennary ganglion into the brain, with chilopods. Other characters of *Hanseniella,* as the absence of eyes and the presence of only a single pair of tracheae (cephalic), are specializations which are probably adaptations to its environment of decaying foliage and rotting logs.

The following embryological differences between *Hanseniella* and lepismatids are considered by the author to be the result largely of the difference in relative volume of yolk in their eggs. In *Hanseniella*: (1) Cleavage is total. (2) The germ band is long and from the beginning represents thoracic and abdominal as well as cephalic material. (3) Absence of embryonic membranes; the germ band does not sink into the yolk. (4) Early eclosion, with subsequent anamorphosis. Actually nutritive value of the yolk rather than volume is concerned here. Information is not available on this subject in insects.

Tiegs (1940), however, deems it erroneous to consider the type of cleavage as simply the mechanical result of the quantity of yolk within the egg. In support of this contention he says that the eggs of symphylans are not unusually small, though cleavage is total. But consider the following comparison. The egg of *Hanseniella* is spherical, averaging 0.37 mm. in diameter; the long diameter of the ellipsoidal egg of *Thermobia* averages 1.00 mm., the short diameter 0.80 mm. At hatching, *Thermobia* measures 1.5 mm. long, exclusive of appendages. We deduce that *Hanseniella* also measures close to 1.5 mm. long at hatching, for the following reason. The circumference of a sphere 0.37 mm. in diameter is 1.2 mm. The body of the embryo is curved in a circle around the entire circumference of the egg, but is a little longer than the circumference since the bent head is directed inward. We therefore conclude that the egg of *Thermobia* contains a relatively much larger percentage of yolk than does the egg of *Hanseniella.*

Tiegs further supports his statement by noting that some tiny, yolkless insect eggs have superficial cleavage (Fernando, 1934). But there is no reason to suppose that superficial cleavage, once established, would not be as satisfactory for yolkless as for yolk-rich eggs. We do not consider, however, that this fact invalidates the theory that superficial cleavage was originally developed as an adaptation to large, yolk-rich eggs.

Although only one species of perlarian has been thoroughly studied embryologically, Miller's detailed account (1939, 1940) of *Pteronarcys proteus* reveals a number of similarities between the embryology of this perlarian and that of lepismatids: (1) Practically no cytoplasm is present in freshly laid eggs. (2) The embryonic rudiment represents chiefly cephalic material. (3) The germ band is of the immersed type. (4) The inner layer represents mesoderm only and is produced without the formation of a ventral furrow. (5) The mesoderm of the eleventh abdominal segment shows no coelomic sacs. (6) Transitory appendages appear on the intercalary segment and on abdominal segments two to ten.

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PATCHY DISTRIBUTIONS OF ANT SPECIES IN NEW GUINEA RAIN FORESTS

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While recently engaged in field work in New Guinea the author had several excellent opportunities to study local areal distribution of rain forest ants. During one three-week period in April, 1955, a walk was made from Finschhafen, on the eastern tip of the Huon Peninsula, west for a distance of 45 kilometers through the midmountain rain forests of the Dedua-Hube regions to Tumnang and Laulaunung, thence south for thirty kilometers to Butala on the southern coast. In the vicinity of Lae intensive collecting was conducted over a distance of twelve kilometers in recently continuous lowland rain forest within the triangle formed by Didiman Creek, Bubia, and the section between the Busu and Bupu Rivers.

Areal distributions of individual species were found to be almost universally patchy, despite the external appearance of uniformity of the rain forest environment. Furthermore, in the cases of species abundant enough to be studied in some detail, the patchiness seemed to obtain at two levels of distribution, which for purposes of description here will be referred to as "microgeographic" and "geographic".

Microgeographic patchiness. The species common enough to be studied in detail are also relatively adaptable, occurring usually in spots of variable canopy density (see below) and sometimes in more than one major forest type (e.g., *Leptogenys dimunuta* (Fr. Smith), which ranges from medium lowland rain forest to dry, monsoon forest). In this respect, at least, they seem to be no more specialized than the majority of temperate ant species. At the same time, they show definite preferences for certain local environmental con-

Explanation of Plate 3

Plate 3. Primary medium-aspect rain forest near the lower Busu River, Northeast New Guinea. A bulldozer trail cuts through the lower left hand corner of the picture.

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ditions. At the Busu River and in other lowland rain forest sites investigated, ant species tended to be segregated into local areas, sometimes a hectare in extent or less, which could be distinguished from adjacent areas by their specific canopy densities. When the total range of possible canopy densities at the Busu River, from the open aspect that fringes savanna areas, to the most closed aspect, ordinarily found covering sloughs, was arbitrarily divided into three divisions (open, medium, dense) and their faunas studied, the following microgeographic segregation of ant species was noted.

"Open rain forest". (Plate 5) Broken canopy; considerable ground insolation; leaf litter 2 to 15 cm. thick; leaf mold present but thin and relatively dry; soil loose, well aerated, and relatively dry; moss scarce on both ground and tree trunks; A-stratum trees generally less than thirty meters high; lianes and plank buttresses much less common than in other two divisions; recumbent vines common on ground; soil and rotting logs generally thoroughly penetrated with dense root and rhizome growth; undergrowth relatively dense; sufficient to make human progress across the forest floor difficult. This is the aspect of old second-growth forest and may be created naturally by the fall of large forest trees or, in mountainous areas, by rockslides. It is also a more or less permanent feature of the fringe of forest, generally one to two hundred meters wide, that borders savanna areas. Occasional spots deep within rain forest approach the open aspect even though an immediate cause, such as a large fallen tree, is not in evidence. Ant species that appear to reach their maximum density in open rain forest at the Busu River included *Platythyrea parallela* (Fr. Smith), *Diacamma rugosum* (Le Guillou), *Odontomachus simillimus* (Fr. Smith), and *Cardiocondyla paradoxa* (Emery). In the canopy of the open forest, species of *Crematogaster,* especially subgenus *Xiphocrema,* and of *Technomyrmex* increased generally, while those of *Iridomyrmex* decreased.

"Medium rain forest". (Plates 3, 4). By far the largest lowland area in the Lae area is covered by forest of the following aspect: closed canopy; ground insolation slight;

leaf litter as in open aspect: underlying leaf mold rich and moist; soil loose, well aerated and drained and relatively moist; moss common on the surface of the ground, on rotting wood lying on the ground and on tree trunks; A-stratum trees average 40 meters or more in height; plank buttresses common; lianes and epiphytes abundant; under growth sparse, making human progress across the forest floor easy. The majority of endemic ant species are concentrated in this division. Examples of genera that reached maximum density (in 1955) on the floor of the Busu forest included *Ponera, Myopias, Ectomomyrmex, Pheidole, Strumigenys, Rhopalothrix, Myrmecina,* and *Pristomyrmex.* In the canopy *Iridomyrmex* heavily predominated.

"Dense rain forest". Closed canopy; little or no ground insolation; leaf litter thin, with one-quarter or more of the ground surface completely bare; leaf mold very poorly developed; soil dense, less well drained and moister than in medium forest; parts of the ground surface occasionally holding shallow pools of water after heavy rains; moss abundant, especially on larger rotting logs; A-stratum trees as tall as in medium forest; plank buttresses common; lianes and epiphytes abundant; undergrowth very sparse, even more so than in medium forest. Ants reaching maximum density in various strata of this division at the Busu River included some species of *Pheidologeton, Tetramorium, Leptomyrmex* and *Iridomyrmex.*

Careful analysis would probably reveal many finer details of microgeographic segregation than those indicated here, for the rain forest is an extraordinarily complex mosaic of local habitats, exhibiting seemingly endless nuances and combinations of erosion states, growth and death of vegetation, composition of leaf mold, and other environmental features. Ant species did not appear to be limited to any of these particular divisions within the rain forest proper. At most, the divisions probably serve as density foci, from which the species are constantly pressing out into adjacent, less favorable habitats,

Geographic patchiness. Ant species apparently show extensive and unpredictable variation in population density over short geographic distances above and beyond that already

noted with respect to microgeographic habitat segregation. This phenomenon was first observed in the Hube area of the Huon Peninsula, where, through a few kilometers distance in seemingly uniform mid-mountain forest, dominant species of the genera *Aphaenogaster* (*Planimyrma*), *Meranoplus,* and *Leptomyrmex* showed conspicuously irregular density patterns. The impression was gained that even within the most favored habitats these species showed irregular density patterns. This type of discontinuous distribution is superimposed on the mosaic, habitat-correlated microgeographic patchiness, and the two conditions probably grade into each other. It can be predicted that superimposition of the two levels of patchiness will result in very irregular and complex individual species distributions, which in turn will have a profound effect on the differentiation of local faunas at localities separated by as little as a few kilometers distance. Such an effect was in fact observed in the lowland rain forests of the Lae area, as described below

Differentiation of local faunas in the Lae area. In 1955 most of the area to the north of Lae and east of the nearby Busu River was covered with a mixture of primary and secondary rain forest, with occasional savanna enclaves. Native villages were not numerous, and native agriculture had not made serious inroads into the forest. In the vicinity of Bubia, to the northwest of Lae, extensive land was under cultivation, partly by the Government Agricultural Experiment Station, but even here the forest was still partly intact, and primary tracts were still accessible[1].

[1] According to both Mr. Henry G. Eckhoff and Mr. Carl M. Jacobson (pers. commun.), who were among the first European settlers of the Lae district, extensive clearing of the forests of this area is a comparatively recent event. Prior to 1925 the only European settlement was the mission station at Malahang, on the coast near Lae. In 1925 a small amount of ground was cleared at Didiman Creek to establish the Goverment Agricultural Experimental Station. Between 1925 and 1930, further clearing proceeded in the vicinity but was still restricted to the present town limits of Lae. Mr. Eckhoff, who arrived in 1928, states that in 1929-30, "My wife and I were the only residents of Lae other than the air freighting companies. There were no other agricultural activities". The next principal development was the establishment of a poultry farm just outside the Lae township by Mr. Jacobson. During the Second World War a road was built from Lae through Bubia to the airfield at Nadzab. Since 1945 clearing for agricultural purposes has proceeded to a limited extent of either side of this road.

Three localities within this forested area were chosen as sites of intensive collecting (see figure 1). The Busu-Bupu forest was the least disturbed of the three; lumbering operations had commenced in the collecting area only the year before, and most of the forest seemed in primary condition. The Didiman Creek site contained a tract of forest, at least partly second-growth in nature, that had been preserved within the Government Agricultural Experimental Station on the northern edge of Lae. At Bubia, extensive forest tracts, primary at least in part, extended to the east of the Jacobson Plantation. The forest tracts at these three localities represent relict segments of what can reasonably be assumed to have been continuous, predominantly primary lowland forest as recently as thirty years ago. Bubia and

TABLE I.

	Bubia	Didiman Cr.	Busu R.
Cardiocondyla paradoxa Emery	X	XX	XX
Crematogaster (*Acrocoelia*) *irritabilis* (Fr. Smith)	X	XXX	—
Crematogaster (*Rhachiocrema*) sp. nov.	—	XX	—
Tetramorium validiusculum Emery	XXX	X	XX
Tetramorium ornatum Emery	—	XX	XX
Triglyphothrix fulviceps Emery	—	XX	XX
Aphaenogaster dromedarius Emery	—	—	XX
Meranoplus hirsutus (Fr. Smith)	X	—	XX
Leptomyrmex fragilis (Fr. Smith)	XX	—	XX
Pseudolasius breviceps Emery	XXX	XX	X

Subjective estimates of relative abundance of some dominant ant species at three neighboring localities in New Guinea. A dashed line means absent, or at least never observed; a single X, present but collected only once or twice; double-X moderately abundant; triple-X among the two or three most abundant species at the locality. Since collecting trips were wide-ranging, these estimates reflect most closely the relative abundance of colonies, rather than number of workers or biomass. Further explanation in text.

Busu-Bupu regions were almost connected by continuous forest even as late as 1955. There is no reason to believe

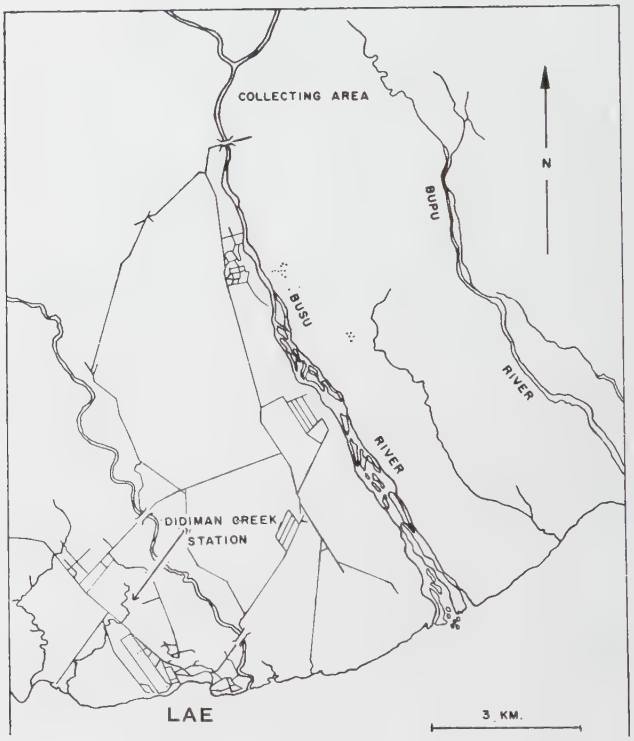

Figure 1. Map of the Lae area in 1955, showing Didiman Creek and the Busu-Bupu area, two of the collecting stations studied with respect to local distribution of species. The third station, Bubia, is located 12.5 kilometers to the northwest of the town of Lae.

Explanation of Plate 4

Plate 4. Floor of primary medium-aspect rain forest near lower Busu River. An overhead tree has just been felled to allow in an unusual amount of sunlight. The exposed portion of the machete is approximately 20 inches, or 50 centimeters, in length. The greatest concentration of species and individual colonies to be found anywhere in New Guinea nest in small pieces of rotting wood in this situation.

that the forests at the three localities, or the ant faunas in them, had been seriously disturbed by man. All three localities contained rich endemic Papuan faunas, with virtually no infiltration of introduced species.

Subjective impressions of the relative abundance of several of the dominant ant species are presented in Table 1. In each of the three localities, all of the major microgeographic areal divisions were studied. Each locality was visited at least twice during the author's two month stay in the Lae area, and a minimum of four days devoted to intensive collecting. Under these conditions, only the commonest species could be compared, but differences in local abundance of these were so striking that it seems safe to predict that similar patchy distributions are exhibited by other, less dominant members of the fauna.

Discussion: The Evolutionary Implications of Patchiness

In any appraisal of comparative ecology, the New Guinea ant fauna is to be characterized first of all by the exceptional richness of its species and the great size of its biomass. The present study has shown that in addition to sheer size, an additional factor adds greatly to the total faunal complexity. This is the discordant patchy distribution of individual species. The fractioning of species into small subpopulations that are partially isolated from one another probably results in relatively high rates of evolution, whether through random drift or differential selective pressures or both (see for instance Kimura, 1955, and Ford, 1955). Moreover, as a result of discordant patchiness, no two localities harbor exactly the same fauna. Considering that several hundreds of species are thus involved, it is clear that the spatio-temporal structure of the entire New Guinea fauna must present the appearance of a great kaleidoscope. The effects of such a structure on the evolution of individual species of

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Explanation of Plate 5

Plate 5. Floor of primary open-aspect rain forest near the lower Busu River. The undergrowth at this spot is made up preponderantly of an unidentified species of *Selaginella*.

ants, as well as of other kinds of animals, must be considerable. It very possibly hastens the genetic divergence of local populations and plays an important role in the "exuberance" and amplitude that characterizes evolution in the tropics. Probably as the fauna increases in size, in passing from temperate to tropical areas or from small islands to large ones, the diversifying effects of a kaleidoscopic population structure increase exponentially.

There is abundant evidence that similar features of population structure occur in other groups of organisms in tropical forests. Aubreville (1938), in his "mosaic" or "cyclical" theory of regeneration, has described a kaleidoscope pattern in forest trees of the Ivory Coast. Richards (1952) doubts whether the mosaic theory holds for all rain forest associations, but accepts its validity in special cases where certain conditions have been met.

> "The poor regeneration of the dominant species in African Forests seems in all probability to indicate that the composition of the community is changing. If the forest is in fact 'untouched and primitive', as Aubreville claims . . . . the changes must be cyclical as the Mosaic theory implies. On the other hand, if the community has undergone disturbance in the past, the present combination of species [in a given sample plot] may be a seral stage and the changes part of a normal (not cyclical) process of development toward a stable climax".

Moreau (1948) finds patchiness a common feature in the distribution of rain forest birds in Tanganyika. Where a species is absent from a locality, it is usually replaced by a related species (from the same family), but not always, leaving some inexplicable gaps. The following example is typical:

> "Nearly all the montane forests of eastern Africa from Kenya southward are occupied by one or both of the little barbets, *Pogoniulus bilineatus* and *Viridobucco leucomystax*. On Hanang Mountain, where both these species are missing, *Pogoniulus pusillus*, normally a bird of deciduous trees at lower altitudes, appears in the mountain forests

(Fuggles-Couchman, unpublished). But this does not happen in the neighboring forests of the Mbulu District, where the fruit-eating barbets are not represented at all."

Additional examples from other animal groups and other parts of the tropics (as well as the temperate zones) could be cited to show that patchiness is a widespread phenomenon, on both a very local (microgeographic) and broader (geographic) scale. To all such cases Richards' conditions must be applied, i.e., it must be asked whether patchiness has not arisen exclusively as a result of man-made disturbances. But patchiness as a result of natural disturbances, such as tree falls and stream erosion, is a good possibility also, and should be considered in the future. In the author's present opinion, much of the patchiness observed in New Guinea ant populations has actually arisen through natural disturbances, since enclaves of second-growth vegetation are a normal feature of remote, undisturbed forest. This argument has been taken up in somewhat more detail elsewhere (Wilson, 1959).

Summary

The population structure of individual Papuan ant species is shown to be generally irregular. Patchiness exists at both a local, clearly ecological level, and a broader, "geographic" level not easily correlated with environmental influences. The combined irregularities in the distributions of multiple species result in distinct shifts of faunal composition and relative abundance over distances of only a few kilometers even in relatively continuous, homogeneous rain forest. The theoretical implications of discordant patchiness with respect to rapid evolution are discussed.

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A *FORMICA* SLAVE-MAKER RAIDING THE NEST OF A MYRMICINE ANT

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Slave-making *Formica* of the *sanguinea* group normally raid the nests of *Formica* of the *fusca, pallidefulva* or *neogagates* groups to obtain pupae to be reared into slavery.

Occasionally, *F. sanguinea* group species have been seen to raid other formicine genera, especially *Lasius,* and Wheeler (1905, Bull. Amer. Mus. Nat. Hist. 21: 11) even recorded a raid on a nest of *Myrmica* (subfamily *Myrmicinae*) species that he watched in Connecticut. Raids by *Formica* on myrmicines apparently are rare occurrences, so the circumstances of such a raid are worth reporting.

On August 22, 1958, at Brown County State Park, Indiana, I witnessed a raid by *Formica subintegra* Emery on a nest of the much smaller myrmicine ant *Aphaenogaster rudis* Emery. The nest entrances of the raiders and the victims were simple holes situated only about one meter apart in the bare clay soil of a hilltop campground, shaded by hickories and a few oaks. The raid was first noticed at about 3 P. M., about 3 hours after a heavy rain had ceased. The sky was partly cloudy, and the air temperature stood at about 70°F.

Most of the visible activity occurred in and around the entrance to the *A. rudis* nest. Six dead or badly maimed *rudis* workers lay near the entrance, accompanied by one crippled *F. subintegra* worker. One *subintegra* worker grappled with a *rudis* worker and put it out of action while I watched. At irregular intervals, *subintegra* workers emerged, most of them carrying a pupa or a dead or struggling worker of *A. rudis,* with which they returned directly to their own nest and entered there. Two *subintegra* workers carried folded-up workers of their own species; when disturbed, these workrs dropped their burdens, which proved to be active and apparently unhurt.

Around their nest entrance, at some distance, circled a few *Aphaenogaster* workers, mostly each carrying one of their own larvae or pupae. Their behavior resembled that of *Formica* slave species when being raided by *F. subintegra.*

Also running in the general vicinity of both nests, but not seen to participate directly in the raid, were a few workers of *Formica fusca* (*s. lat.*), all of them slave members of the *F. subintegra* colony.

The raid was under observation for about one hour, and my impression was that it had been in progress for some time before I first saw it. It compared with the terminal stages of other raids I have seen *F. subintegra* make on other *Formica* species. The raid was terminated by heavy rain in the early evening, and was not continued on the next day.

On partial excavation, pupae and dead or injured workers of *A. rudis* were found in the *subintegra* nest, but there were no *Aphaenogaster* workers present and intact that seemed to be acting as slaves. Therefore, I concluded that the raid would probably not be successful in introducing the *Aphaenogaster* into adult slavery.

In the present observation, it is not known whether the captured pupae or adult *Aphaenogaster* workers were eaten by the *Formica* raiders. But even if they were, such behavior is not necessarily of more than routine significance, since ants will eat their own pupae under various circumstances.

My own interpretation of the raid is based on the apparent lack of nests of suitable slave species of *Formica* in the campground, and the abnormally exposed nature of the *Aphaenogaster* nest. Since *F. subintegra* workers had been seen foraging singly over the area for several days previous to the raid described, I suspect that these represented scouts that were unsuccessful in locating suitable *Formica* spp. nests to plunder. Under such conditions, the pressure for the release of raiding activity may have been high, so that eventually even such a poor target as the *Aphaenogaster* nest came to represent a stimulus sufficient to start and maintain a raid.

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